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## Short Communication

# Unusual Flowering Shoots of *Damnacanthus* (Rubiaceae)

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The spine of *Damnacanthus* has been interpreted as a metamorphosed leaf or a lateral branch. There is a hypothesis that a pair of spines is modified inflorescence by the observation in which vegetative and reproductive branching units are comparable to each other. Our observations of various transitional forms between the spines and the pedicels in *Damnacanthus* agree with the hypothesis.

Key words: *Damnacanthus*, Rubiaceae, spine, thorn

A spine, a stiff, sharp-pointed structure, is often interpreted as metamorphosed organs: shoots, leaves, stipules, flowers, and so on. For example, the spines of cacti (Cactaceae) represent modified leaves (Bell 1991). *Barleria prionitis* (Acanthaceae) has bract spines (Bell 1991). In *Carissa grandiflora* (Apocynaceae), a pair of spines is homologous to an inflorescence (Cohen & Arzee 1980).

*Damnacanthus*, a small shrubby genus of Rubiaceae, is characterized by heterophylly associated with the sympodial branching pattern and spines. As Yamazaki (1987) and Robbrecht *et al.* (1991) observed, each sympodial element of *Damnacanthus* comprises three nodes (Fig. 1A). On the first node present a pair of prophylls (the first leaf pair of a sympodial element), which develops into small leaves or remains like scales. On the second node present a pair of foliage (larger) leaves. A new sympodial element originates from the axil of a foliage leaf. A pair of spines on the top of the shoot, arranged at right angles to the foliage leaf-pair, may represent lateral segments at the third node. The internode between the second and third nodes is extremely shortened. A sympodial element terminates its development in this node.

For many years, various morphological interpretations of the spines of *Damnacanthus* have been proposed. Schumann (1891) mentioned that a spine of *Damnacanthus* was homologous to a lateral branch unusually subtended by a stipule. However, no plant with a lateral branch subtended by a stipule has been reported (Kumazawa 1979). Johansson (1987) explained in a brief description of *Damnacanthus*, that narrow stipules developed into spines. In fact, stipules occur independently from spines (Fig. 1), although stipules are often dropped earlier according to our observations. Kumazawa (1979) observed a cylindrical vascular bundle in a

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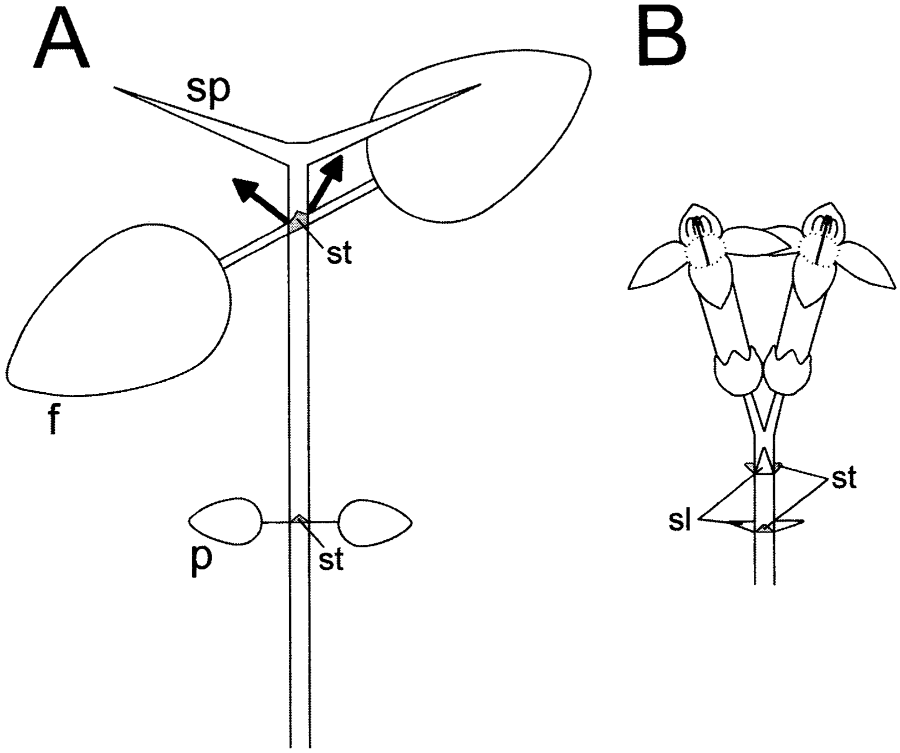

FIG. 1. Schematic of sympodial branch unit (A) and inflorescence (B) of *Damnacanthus indicus*. Actually, the node between foliage leaves and spines are highly shortened and the inflorescence shoot is very short. *f*, foliage leaf; *p*, prophyll; *sl*, scale-like leaf; *sp*, spine; *st*, stipule. Arrows show axillary buds (new sympodial elements) occurring from the foliage-leaf nodes.

spine of *Damnacanthus*, and explained a spine of *Damnacanthus* as a metamorphosed leaf. Yamazaki (1987) examined the nodal anatomy of young shoots of *D. indicus* var. *major*, and found that the structure of vascular bundles entering a leaf was different from that entering a spine. A usual leaf trace entered a leaf, whereas a cylindrical vascular bundle entered a spine. He interpreted that a spine was a lateral branch adhered by a subtending leaf to the base because he could observe neither a leaf trace nor a leaf gap of the expected subtending leaf.

Robbrecht *et al.* (1991) suggested that a sympodial element of *Damnacanthus* was homologous to an inflorescence shoot (Fig. 1). They indicated that an inflorescence shoot, also comprising three nodes, is comparable to a sympodial element. They explained that the two pairs of scales and a pair of flowers in an inflorescence shoot correspond to a pair of prophylls, a pair of foliage leaves, and a pair of spines, respectively. Therefore, they hypothesized that the paired terminal flowers were homologous to a pair of spines.

## Materials and Methods

We observed flowers of four taxa of *Damnacanthus, D. biflorus* (Rehd.) Masam., *D. indicus* C. F. Gaertn. var. *indicus*, D. *indicus* C. F. Gaertn. var. *microphyllus* Makino, and *D. macrophyllus* Siebold ex Miq., collected in the field (refer to the Appendix) and fixed in FAA (10% formalin, glacial acetic acid and 70% ethanol mixed respectively by 5: 5: 90 in volume), under a stereoscopic microscope (Leica Microsystems, M420, Wetzlar, Germany).

## Results and Discussion

In *Damnacanthus* normally, an inflorescence shoot

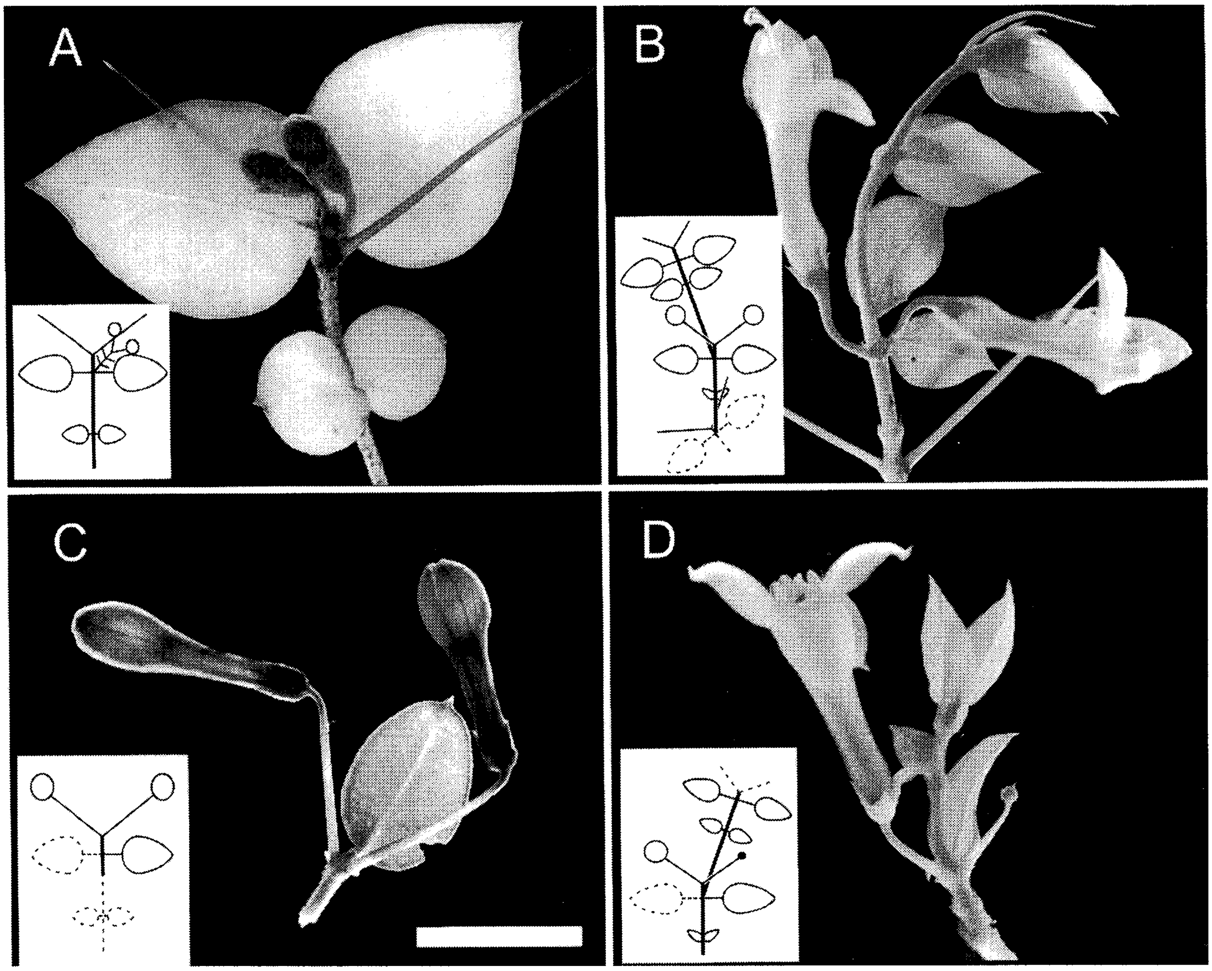

FIG. 2. Normal (A) and unusually arranged (B-D) flowers of *Damnacanthus indicus* and the schematic explanations. A. Normal inflorescence with a pair of flowers originates from the axil of a foliage leaf. B. Two solitary flowers originate at the third node from which otherwise spines normally occur, and a young shoot developing from the axil of a foliage leaf. C. Pedicels of two solitary flowers elongate and are stiffened like spines. D. Flower occurs at the tip of stiffened pedicels. One flower is insufficiently developed. Bar = 1 cm.

terminated by a pair of flowers arises from the axil of a foliage leaf like a new sympodial element (Fig. 2A). However, we found some unusually arranged flowers. In one case, a pair of solitary flowers developed at the third node from which otherwise a pair of spines occurs (Fig. 2B). This type of irregularity was found in all taxa observed. In another case, in *D. indicus* var. *indicus* and var. *microphyllus*, the pedicels of two solitary flowers were elongated and stiffened like spines (Fig. 2C). In addition, Figure 2D shows an insufficiently developed flower of *D. indicus* var. *microphyllus* occurring at the tip of a spine-like pedicel. Because the paired flowers in an inflorescence usually mature and open on the same day, the smaller one is not a flower bud, but a flower rudiment.

Robbrecht (1988) reported that the tip of a spine of *Catesbaea spinosa* (Rubiaceae) sometimes develops into a flower. He could not found such a case in *Damnacanthus*, but speculated the inflorescence origin of the spines of *Damnacanthus* because the reproductive and the vegetative shoots are comparable (Robbrecht *et al.* 1991). Here we first reported various transitional forms between the spines and the pedicels in *Damnacanthus*, and these observations of exceptional flowers agree with the hypothesis by Robbrecht et al. (1991), that a spine is homologous to a flower. The interpretation about spines of *Damnacanthus* by Yamazaki (1987) is basically the same as the hypothesis by Robbrecht *et al.* (1991), because a determinate lateral branch can be comparable to a flower. But the hypothesis by Robbrecht *et al.* (1991) is more important, because they indicated the homology between a sympodial element and an inflorescence shoot.

Another morphological peculiarity is that each spine does not have a subtending leaf in *Damnacanthus*. The unusual flower which originates instead of a spine also does not have a bract. Even in a normal inflorescence shoot of *Damnacanthus*, there is no lateral segment on the pedicels. This situation is quite strange, because a lateral branch generally arises from the leaf axil in plants (Kumazawa 1979). The similar dichotomous spines of *Carissa grandifolia*, a spiny species of Apocynaceae, are subtended by a bract (Kumazawa 1979, Cohen & Arzee 1980). Yamazaki (1987) explained that a bract of *Damnacanthus* was cohered to a spine, although he could not find evidences supporting his interpretation. Early stages of development of the spine should be observed.

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## Appendix

Collection data of the observed materials of *Damnacanthus*.

| Taxa | Locality | *Voucher no. (KYO) |
|---|---|---|
| *D. biflorus* | Mt. Nishime, Kunigami-son, Okinawa Pref., Japan. | *Naiki 5688* |
| *D. indicus* var. *indicus* | Honen'in, Kyoto City, Kyoto Pref., Japan. | *Naiki 5689* |
| *D. indicus* var. *microphyllus* | Ise City, Mie Pref., Japan. | *Naiki 5690* |
| *D. macrophyllus* | Mt. Kiyomizu, Kyoto City, Kyoto Pref., Japan. | *Naiki 5691* |

*preserved in FAA.

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